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Similar Mechanical Forces in Hemimandible Goat Breeds

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ABSTRACT

The mammalian mandible is generally seen as a functional unit as a lever during biting. Allometry can be an important factor that contributes to adaptative traits and its variation. The purpose of this study was to determine if there is an allometric relationship in goat hemimandible. For this purpose, seven hemimandibles belonging to wild Capra pyrenaica and 43 more belonging to different domestic goat breeds were studied. Digital photographs were used to obtain two distances: from the temporo-mandibular to the middle of the cheek teeth row, and from the temporo-mandibular articulation to the bottom of the angular process. Our analyses determined that goat hemimandibles exhibit positive allometry (r2=0.658), which hints at fundamental constraints in goats due to their size differences. Nevertheless, in view of methodological constraints (exclusively morphometrical data, small sample size, lateral landmarks…) we caution that this similar functional pattern of mandible can not exclude adaptative patterns.

Keywords: Static allometry; Bite force; Mandible strength

Introduction

Ruminants eat coarse vegetation, such as leaves of grasses and trees, which have tough fibers and a high cellulose content. After partially chewing the food, they swallow it and it is fermented with cellulose-digesting bacteria in the rumen. Posteriorly this material will be regurgitated and chewed further to release more nutrients and to increase the surface area of the vegetation in order to facilitate the broke down by ruminal bacteria.

Grinding of this tough fibrous material is accomplished with massive cheek teeth (premolars and molars)[1]. Two muscles, the temporalis and the masseter (pars superficialis), which originate on the skull, apply forces to the hemimandible in chewing [2]. Thus the mandible can be considered a lever system which applies force in food handling and summarization [3]. In the herbivores, the relative scale and morphology of the mandible can have profound consequences for the energetic efficiency of chewing.

In terms of the physics of mandible, mandible operates as a lever of sorts. A lever consists of a pivot point (the temporomandibular joint TMJ), and two lever arms. An in-lever arm connects the pivot to the point where an "in-force" (Fi) is applied by the muscle. An out-lever arm connects the pivot to the point where an "out-force" (Fo) is applied by the teeth to the food. As a general rule, Fo (chewing force) can be increased by decreasing the out-lever arm and increasing the in-lever arm. The force-multiplying effect of a lever is characterized by the ratio: F0 / Fi.

The higher the mechanical advantage, the greater Fo. Strongly inspired by the teaching document "Lever Mechanics and Feeding Diversity in Carnivora" (available at https://www.mtholyoke.edu/courses/.../Lab7-carnivores.pdf, accessed on December 2016)As a measure of the in-lever arm of the masseter we utilized the distance from the TMJ to the bottom of the angular process, which can be called the In-Lever Arm (ILA). As a measure of the out-lever arm for the chewing teeth, it is possible to use the distance from the TMJ to the middle of the tooth row, which can be taken as the line between the PM3 and M1. We will call this the Out-Lever Arm (OLA).

Allometry designates "the relationship between changes in shape and overall size" [4]. Julian Huxley and Georges Teissier coined this term in 1936 [5]. It is well known that animals are rarely isometric, i.e. their organs usually do not scale in a linear fashion with their bodies. Because allometry can be related to age or developmental stage, across individuals, across populations and across species [6], at least four different concepts of allometry are usually distinguished:

1. ontogenetic allometry, which refers to relative growth in individuals;
2. phylogenetic allometry, which refers to constant differential growth ratios in lineages;
3. intraspecific allometry, which refers to adult individuals within a species or a given local population;
4. interspecificallometry, which refers to the same kind of phenomenon among related species [7].

Categories (1) and (2) are commonly characterized as "dynamic" or "truly temporal"; categories (3) and (4) as "static" [7].

In his largely cited paper, Huxley formulated the law y=bxk where: y is the magnitude of the differentially growing organ; x, the body size; k, the constant differential growth-ratio; and b, the constant (origin index)[5]. But the most commonly used allometric equation employs not a linear but a logarithmic scaling of both body size and the size of the organ under study: log (y)=log (b)+k log (x)[6], allowing log-transformed data to be modeled using linear regression. All of these concepts are well reviewed and discussed by Gayon [8]. Positive allometry (i.e. b>1) means that the organ under study carried by larger individuals will be proportionally larger than those carried by smaller individuals [6].

Study of allometry in animals usually relates the size of an organ to some functional property of that organ. From a biological perspective, one could suspect that the morphological variation in herbivores follows essentially an allometric trajectory, a major component of shape variation being thus related to size, or the attainment of adult size (i.e., growth). However, the functional consequences of a possible allometry are still not studied. The mammalian mandible is generally viewed to function as a lever. So the purpose of this study was to determine whether or not the allometric relationship holds for goat hemimandible static allometry (which for the sake of brevity we shall refer to simply as 'allometry' from now on), using a dataset derived from a survey of specimen pictures.

MATERIALS & METHODS

Materials

Seven hemimandibles belonging to wild Capra pyrenaica and 43 more to different domestic goat breeds were studied (African breeds: Kano Brown n=7, Yankasa n=1, European breeds: White Rasquera n=30, undetermined n=5). The hemimandibles of Capra pyrenaica (n=7) and undetermined breed specimens (n=5) are deposited in the Natural History Museum of Barcelona (Catalonia, Spain). Kano Brown and Yankasa skulls (n=8) were from the Department of Veterinary Anatomy, University of Agriculture, Makurdi (Nigeria), and the rest (n=30), are from the collection of the Department of Animal Production of the University of Lleida (Catalonia, Spain). Sex was not available for all specimens, but this variable was not taken into account for the present purpose as authors have found no compelling publication for the sexual mandible differences in this Capra, so it was considered no significant functional variation between sexes.

Image acquisition

Image capture was performed with different digital cameras but in all cases the focal axis of the camera was parallel to the left lateral aspect of each hemimandible. A scale bar was used in this process. Three landmarks (i.e. two-dimensional coordinates), assumed to be homologous and topologically equivalent, were plotted on each hemimandible using TpsDig, v. 2.16 software [9], which allowed to place landmarks on images and also record scale factor. Landmarks used in this study were chosen to perfectly describe (1) the point between the PM3 and M1, (2) the head of condylar process, and (3) the angle of hemimandible as shown in Fig. 1. These landmarks were considered enough to capture basic functional information of the mandible. The real distances between (1) to (2) (OLA) and (2) to (3) (ILA) were then calculated using PAST—Paleontological Statistics Software Package for Education and Data Analysis, v. 2.17c [10], using the same distance control (50 mm) in all pictures. Tps series and PAST are available over the Internet by FTP from the "morphmet" directory at life.bio.sunysb.edu or via the WWW at http://life.bio.sunysb.edu/morph/.

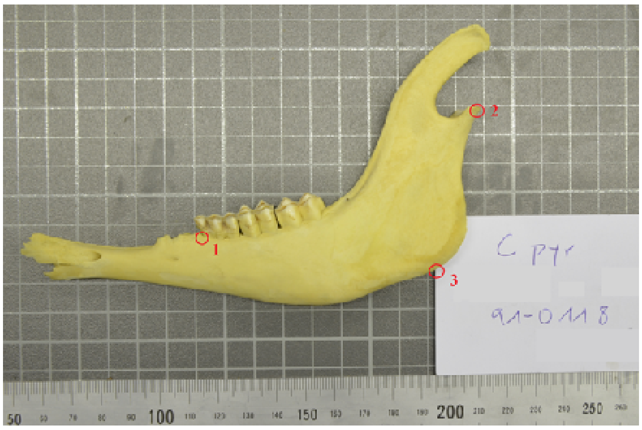

Figure 1: Used points for estimating distances: (1) point between PM3 and M1 (in this picture, premolar series is missing), (2) the head of condylar process, (3) the angle of hemimandible

Regression

Linear regression (ordinary least-squares, which minimizes the squared residuals) between OLA and ILA was estimated using log-transformed values using the cited software PAST.

For both groups (Capra pyrenaica and domestic goats) the log–log regressions on analysis of covariance (ANCOVA) was performed to determine whether the slopes and intercepts differed significantly. To determine whether the regression line was underestimated or overestimated we used a Wilcoxon signed rank test to examine the differences between the actual log ILA values and those predicted by the regression line.

RESULTS AND DISCUSSION

According to an ANCOVA, the slope and of the regression line for Capra pyrenaica and domestic goats did not differ significantly (F=2.875, p>0.05) as shown in Figures 2 and 3 shows the estimated regression line for all samples. The significant regression (p<<0.0001) presented a slope of 0.807, the intercept was 0.175 and the r2 value was 0.658. A comparison of actual log axial ILA weights with those predicted from the regression line using a Wilcoxon signed rank test showed that the probability that these were drawn from the same population was not significant (W=679.5, p=0.505).

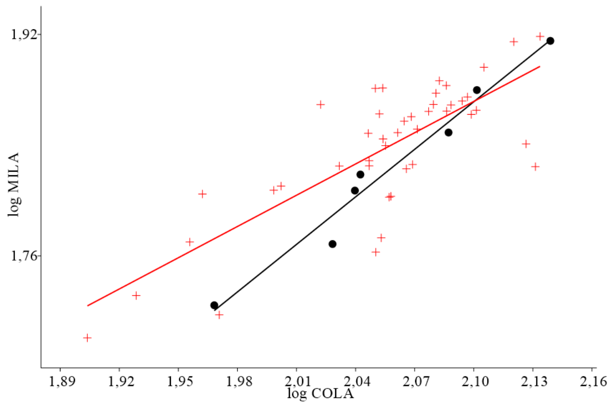

Figure 2: Regression lines for Capra pyrenaica (dots) and domestic goats (crosses). They did not differ (F=2.875, p>0.05)

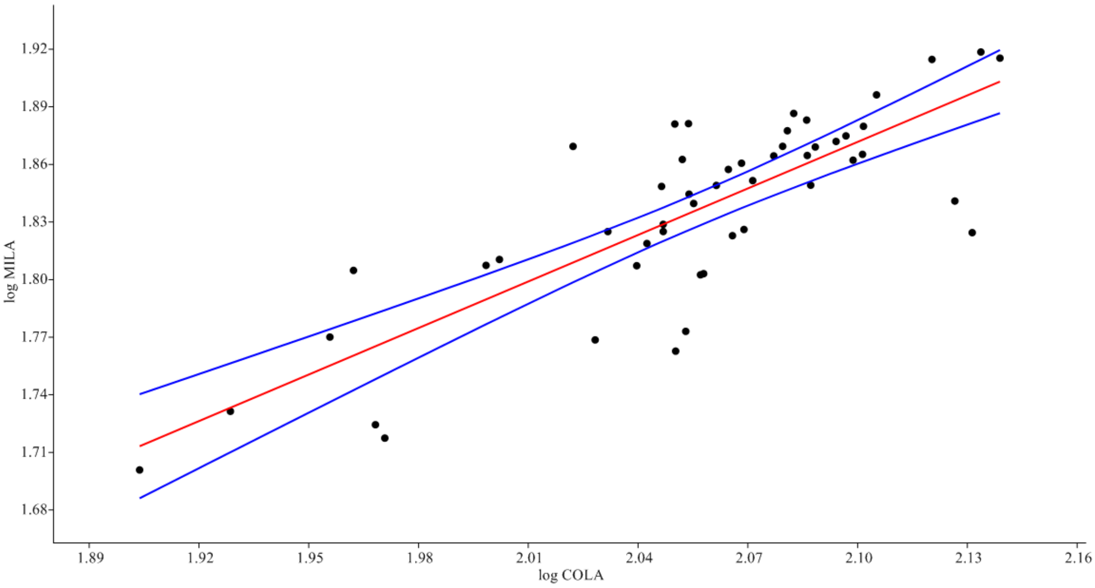

Figure 3: Double logarithmic plot between Masseter In-Lever Arm (MILA) and Chewing Out-Lever Arm (COLA). The solid line is the ordinary least-squares regression line log (y)=log (0.175)+0.807 log (x), which was used for the calculation of residuals. Because the data are plotted on a log–log scale, the slope of the fitted line gives an estimate of the exponent k discussed in the text. Each data point represents each specimen

These results would suggest that hemi-mandible mechanics does not change as a consequence of the increase in size. But our conclusion must be viewed only as initial results, because data were solely done in the lateral projection. In fact, it would be necessary to analyze the forces acting on the mandible in the frontal projection, particularly during unilateral biting (which is clearly difficult using only two-dimensional morphometrical data). In addition, an analysis of the strength of the condylar neck, which is not possible using only data we worked with, would demonstrate if this structure is strong enough to withstand the expected reaction force during lever action. Moreover, no conclusions if goat mandible acts as a lever or link can be deduce, as different researches suggest different conclusions[11], based essentially on two assertions: (1) the resultant of the forces produced by the masticatory muscles always passes through the bite point; (2) the condylar neck and/or the temporomandibular joint is unsuited to withstand reaction forces during biting. So we caution that detected similar functional pattern of mandible may not exclude adaptative patterns.

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